

INTERPRETATION OF TENTACULAR CLUB STRUCTURE IN *STHENOTEUTHIS OUALANIENSIS* (LESSON, 1830) AND *OMMASTREPHES BARTRAMII* (LESUEUR, 1821) (CEPHALOPODA, OMMASTREPHIDAE)

By

MARTINA A. ROELEVELD

South African Museum, Cape Town

(With 6 figures)

[MS accepted 25 February 1982]

ABSTRACT

The club structure in the family Ommastrephidae is shown to be more easily interpreted if the first dactyl row is taken to be that row in which the ventrolateral sucker is equal to, or larger than, the ventromedial and the carpus is considered to be restricted to the region bearing biserial suckers. All the proximal suckers that may be considered to be quadriserially arranged are taken to pertain to the manus, even when subequal in size.

Using these definitions, the club structure in ommastrephids is found to be remarkably uniform. In the subfamily Ommastrephinae the position of the fixing apparatus is found to be constant within a species if it is defined by the position of the first smooth ringed sucker; its position in *Ommastrephes bartramii* is clearly different to that in *Sthenoteuthis oualaniensis* and other species.

It is shown that the sucker arrangement of the clubs may be related to their function of capturing prey.

CONTENTS

	PAGE
Introduction	249
Historical review	250
Proposed interpretation of club structure	253
Discussion	261
Acknowledgements	263
References	263

INTRODUCTION

Squids (order Teuthoidea) are primarily active predators feeding mainly on fish, crustaceans, and other squids. Prey is captured and held by the circumoral appendages, which consist of eight sessile arms and two tentacles. The sessile arms usually bear suckers or hooks over most of their length and are used to hold the prey while it is being eaten. The function of the tentacles is to capture the prey and bring it within reach of the arms. The tentacles differ from the arms in that they usually have a bare stalk that is very extensible, the length of the tentacle depending on the degree of contraction of the longitudinal muscles. The distal end of the tentacle is expanded to form a club that bears toothed suckers or hooks.

Young & Roper (1968: 197–202) have given a comparative evaluation of the familial characters in the suborder Oegopsida, which includes twenty-three of the twenty-five families of squids. They have pointed out that the structure of the tentacular club is one of the more stable characters used in classification at the familial level and that an understanding of club structure and variation throughout the suborder is essential for the establishment of a coherent classification. Furthermore, the club is not only of primary importance in defining families but is often diagnostic at the generic and specific levels as well. The above authors cite the Ommastrephidae (except *Illex*) as one of the groups possessing the basic or typical club, which occupies a relatively small portion of the tentacle, is at least somewhat expanded and flattened, and is divisible into three distinct areas: the carpus, the expanded manus possessing marginal trabeculate membranes and four rows of suckers, and the narrow dactylus where the suckers become greatly reduced in size (the dactylus also has four rows of suckers in all the ommastrephids except *Illex*, which has eight rows of suckers on the dactylus). In addition, the typical club usually exhibits a more or less distinct pattern of small suckers and knobs that, when held together, form a locking device, the carpal structure or fixing apparatus.

The basic structure of the ommastrephid club, as outlined above, has long been recognized. The precise definitions of the three regions and of a transverse row are less clearly agreed upon, however, and have varied from author to author or have been ignored.

HISTORICAL REVIEW

One of the earliest descriptions of ommastrephid club structure was given by Pfeffer (1912: 374–376), who suggested that the carpus, manus, and dactylus may only be delineated by careful analysis, and pointed out that the suckers of the three regions differ in size and dentition.

Pfeffer found that the suckers on the dactylus are significantly smaller than the rachial (median) suckers of the manus and that in each transverse dactyl row the two ventral suckers are generally larger than the two dorsal ones. This relationship becomes unclear only near the tip of the club and proximally, in transition to the manus region: in the second dactyl row the two ventral suckers are about equal in size but in the first (most proximal) dactyl row the ventral rachial sucker is always larger than the ventral lateral sucker. The dactylus may then be delineated from the manus by the difference in size between the most distal rachial sucker of the manus and the most proximal one of the dactylus, this size difference being much more noticeable on the right club than on the left, since both clubs have an asymmetrical structure. The dactylus may also be separated from the manus by the dentition of the rachial suckers; the lateral manus suckers and the more proximal dactylus suckers resemble the more distal suckers of the arms, whereas the rachial suckers of the manus have a unique form of dentition (i.e. completely different to the dentition of any other sucker of the species).

Regarding the sizes of the carpal suckers, Pfeffer noted only that the rachial sucker is clearly larger than the lateral sucker in the distal carpal rows, but not more proximally. The dentition of the carpal suckers generally resembles that of the large arm suckers.

Pfeffer considered an analysis of club structure to be important because he believed that individual species could be distinguished by the number of quadriserial rows, particularly of the carpus and manus. Pfeffer's concept of a transverse row was as follows: in each quadriserial row the lateral sucker is proximal to the rachial and the dorsal rachial sucker is somewhat proximal to the ventral rachial sucker. This suggests that Pfeffer interpreted an imaginary line passing through the centres of the suckers of one transverse row as forming an arc across the oral surface of the club, rather than an oblique, more or less straight line. Pfeffer also saw all the club suckers of ommastrephids (except *Illex*) as quadriserially arranged, including those of the carpus, though he noted that on the left club the most proximal sucker is missing, so that the proximal quadriserial row of the carpus of the right tentacle corresponds to a triserial group on the left tentacle.

Pfeffer considered that the ommastrephid fixing apparatus, consisting of a dorsal lateral row of alternating knobs and suckers, belongs primarily to the carpus, though continuing on to the manus in many species. He noted that the number of elements of the fixing apparatus varies but that its position is more constant and may be determined by counting the number of suckers proximal to the first (most proximal) knob.

Pfeffer's careful description of ommastrephid club structure is largely valid but his method of club analysis proved very difficult in practice, as he himself pointed out. Whilst delineation of the manus from the dactylus is satisfactory provided that the differences in size and dentition are clear, he relied entirely on dentition to distinguish carpal from manal suckers. But transitional conditions occur, and the dentition of the median (rachial) suckers gradually changes from the carpal to the unique median manus condition and from the latter to the dactyl condition, though the transition from manus to dactylus is more rapid (over about two to three transverse rows) than from carpus to manus. Similarly, the transition in sucker size from manus to dactylus is not always as distinct as indicated by Pfeffer; the transition in sucker size from carpus to manus is very gradual and does not permit the delineation of the two regions by the criterion of relative sucker size.

Pfeffer has pointed out another disadvantage of using sucker dentition to delineate the regions of the club, namely the fact that sucker dentition is only rarely visible *in situ*, so that an investigation of dentition necessitates the dissection of a large number of suckers from several specimens. Clearly determination of the limits of the three club regions and of the number of transverse rows in each region using only the criteria of relative sucker size and arrangement, independent of dentition, would be a distinct advantage.

Pfeffer, using his concept of the transverse row as outlined above, suggested that the number of rows of the manus and carpus may be determined, after the distal limit of the manus has been established, by tracing the rows, one by one, from the clearly quadriserial rows of the manus and proceeding proximally. This is not, however, always possible as the suckers may become displaced due to distortion. Pfeffer suggested that in these cases the total number of suckers on the manus plus carpus be counted and divided by four! Another difficulty in analysing the quadriserial rows of the carpus is due to the progressively wider separation of the more proximal suckers, so that they appear to have an irregular or scattered arrangement.

The different interpretations of ommastrephid club structure by various subsequent authors may best be illustrated by citing some of their descriptions, with particular reference to the carpal region where the main disparities arise. Since these authors described different species, it is necessary to point out that, according to the interpretation of the present author, the species under discussion all have the same basic sucker arrangement but that the fixing apparatus varies as follows: in the subfamily *Todarodinae* the fixing apparatus is represented by a series of knobs, which may be clearly or poorly defined, alternating with toothed suckers; in the subfamily *Ommastrephinae* (except in *Ornithoteuthis* spp.) the fixing apparatus consists of a variable number of alternating knobs and smooth ringed suckers situated along the dorsal edge of the club in the proximal region.

Berry (1918: 236–237) described the club of *Nototodarus gouldi* (McCoy) (*Todarodinae*) as bearing suckers in four rows, the eight large pairs of median manus suckers succeeded by three pairs of evenly diminishing suckers that, with the marginal series, passed imperceptibly into two rows of very small suckers (some four to six pairs) on the carpus. He saw the carpal suckers as tending to occur in alternating but only slightly differentiated sizes, the larger evidently a continuation of the two central rows of the club, the smaller of the marginal rows. The fixing apparatus was sometimes so obscure as to be practically indistinguishable, but where best preserved it found its proximal beginning after the third sucker of the dorsomarginal row and comprised first a small pad, then three large ones in regular alternation with the suckers of this row on the basal portion of the club.

Sasaki (1929), in his monograph on the Cephalopoda of Japanese and adjacent waters, described six species of the *Ommastrephidae*. He recognized that the most proximal suckers of the carpus could not readily be considered as forming transverse rows of four but did not offer a single alternative interpretation. Thus for *Ommastrephes sloani pacificus* (= *Todarodes pacificus* Steenstrup) (*Todarodinae*) he described the eight to eleven carpal suckers as small nearly uniform suckers arranged in three or four rows of 1, 3, 4 or 2, 3, 4 or 3, 4, 4 or 1, 2, 3, 4 in each (Sasaki 1929: 279). In his figure (text-fig. 134B) he illustrated the 2, 3, 4 interpretation.

Adam (1952: 108–109) stated that at the base of the club of *Ommastrephes*

pteropus [= *Sthenoteuthis pteropus** (Steenstrup)] (Ommastrephinae), on the dorsal side, there were three to five rounded papillae alternating with as many small suckers that had smooth horny rings. Proximal to the first papilla there were none to two small suckers, also with smooth rings. At the base of the club the suckers were at first placed in pairs, then in rows of four, followed by the rows of four suckers of the principal part of the club (the manus). Adam found it impossible to establish clear limits for the three groups of tentacular suckers, which comprised two to four rows of four carpal suckers, eight to ten principal and twenty to thirty distal rows.

Voss (1963: 131–132) described the club of *Nototodarus sloani philippinensis* Voss (Todarodinae) as occupying about three-fourths of the total tentacle length. The indistinct carpal section bore about eleven suckers, differentiated by their dentition, that might compose the carpal cluster. Five of these were not in regular order but consisted of a proximal pair, followed by three others in an irregular row. Beyond these the next four were also irregular. The suckers of the manus were in four rows.

Young (1972: 29–30), in describing the club of *Ommastrephes bartramii* (Ommastrephinae), saw the suckers proximal to the manus as irregularly aligned and extending on to the tentacular stalk for a short distance. He described the fixing apparatus as consisting of two to four smooth-ringed carpal suckers alternating with two to four pads, lying at the proximal end of the manus along the ventral margin (clearly a *lapsus calami* for dorsal margin). Proximal to the fixing apparatus there were five to six toothed suckers.

Wormuth (1976), in his revision of the Pacific ommastrephids, saw the club suckers as arranged in longitudinal columns rather than in transverse rows. He described (p. 26) the club of *Symplectoteuthis oualaniensis* (= *Sthenoteuthis oualaniensis*) (Ommastrephinae) as having a carpal region with a differentiated fixing apparatus consisting of three to five knobs alternating with suckers having smooth rings on the dorsal oral surface of the club; the fixing apparatus started basally with a smooth ringed sucker and usually ended distally with a knob. There were three small, slightly dentate suckers on the ventral oral surface of the carpus.

PROPOSED INTERPRETATION OF CLUB STRUCTURE

In the course of examining over 130 specimens of *Sthenoteuthis oualaniensis* and numerous others of the remaining ommastrephid species with a view to a systematic revision of the family, it has been found that the arrangement of suckers and knobs on the tentacular clubs is far more regular than indicated by the above descriptions by previous authors, and that club structure may readily be compared from species to species if the basic ground-plan of sucker arrangement is recognized.

* *Ommastrephes pteropus* and *Symplectoteuthis oualaniensis* were united in the genus *Sthenoteuthis* by Zuev *et al.* (1975: 1475). *Symplectoteuthis* Pfeffer, 1900 (type species *Loligo oualaniensis* Lesson, 1830), thus becomes a junior synonym of *Sthenoteuthis* Verrill, 1880 (type species *Architeuthis megaptera* Verrill, 1878 = *Ommastrephes pteropus* Steenstrup, 1855).

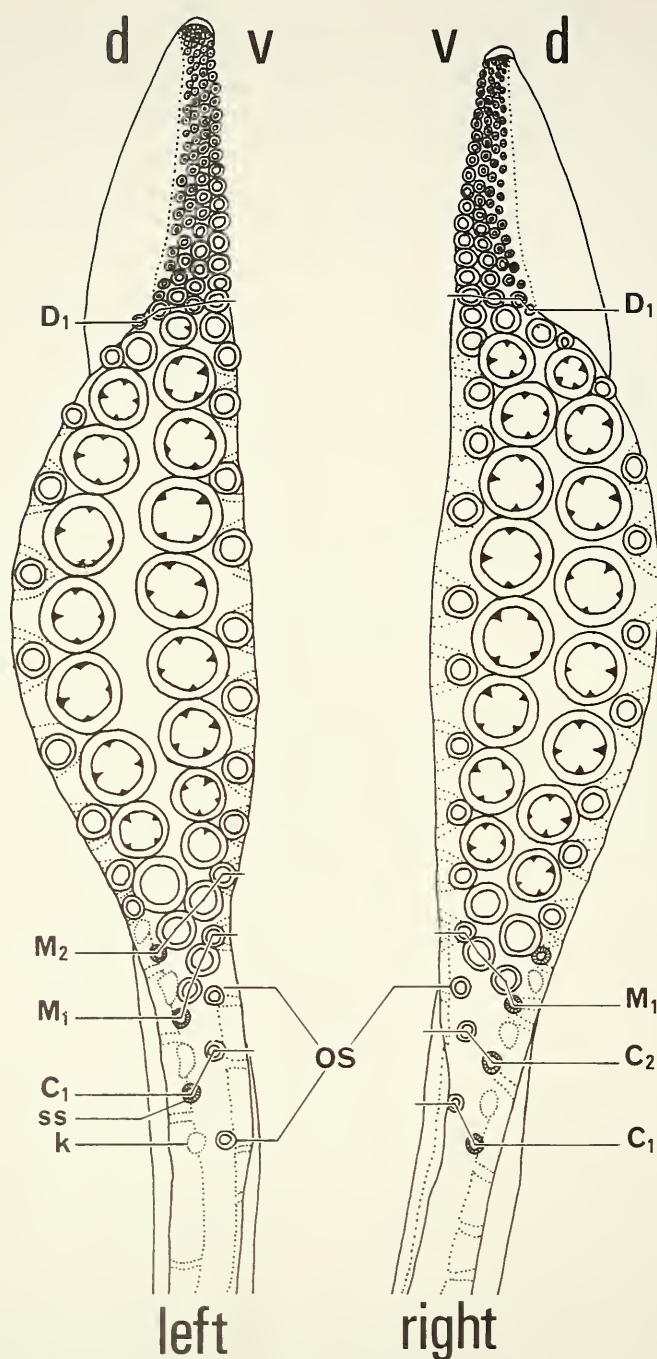


Fig. 1. Semidiagrammatic representation of the tentacular clubs of *Sthenoteuthis oualaniensis*, mature male, mantle length 126 mm. Galathea sta. 420, 10°24'N 126°40'E. C₁, C₂—first and second rows of carpus, d—dorsal, D₁—first row of dactylus, k—knob of fixing apparatus, M₁, M₂—first and second rows of manus, OS—odd (unpaired) suckers of carpus, ss—smooth ringed suckers of fixing apparatus, v—ventral.

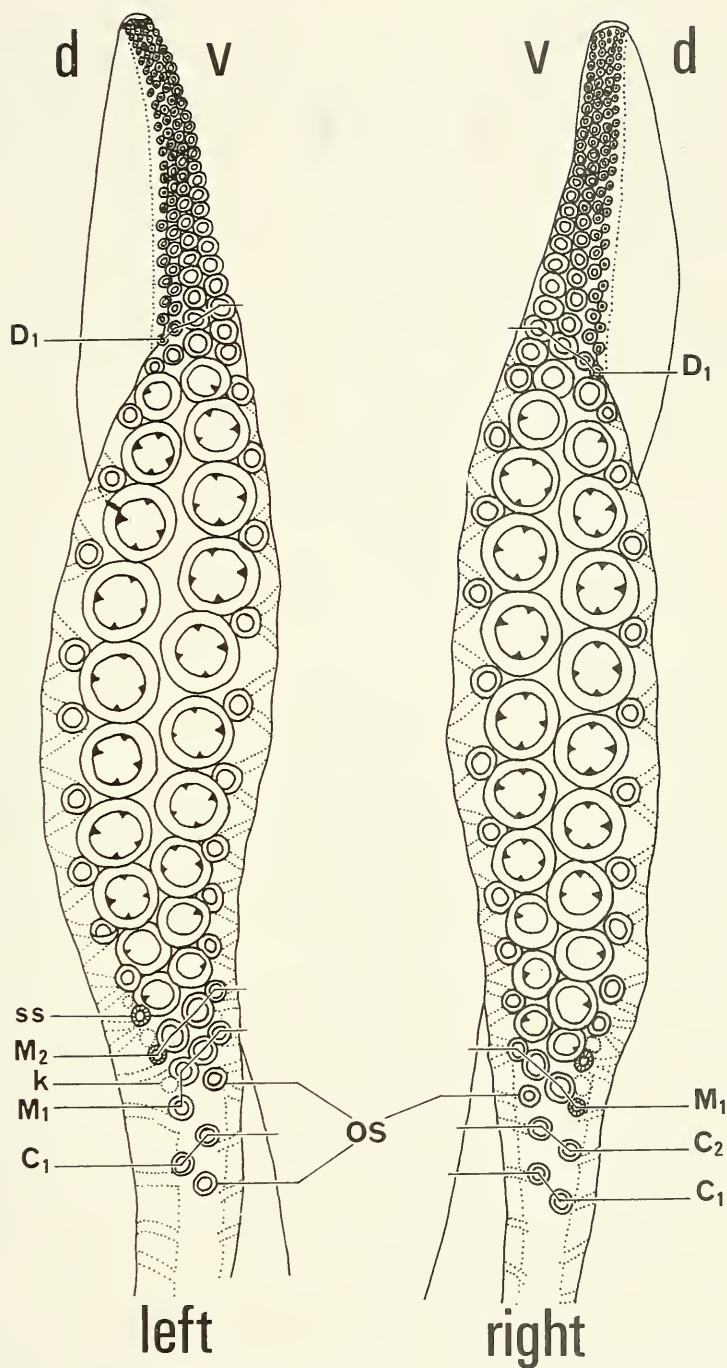


Fig. 2. Semidiagrammatic representation of the tentacular clubs of *Ommastrephes bartramii*, SAM-S241, immature male, mantle length 182 mm, Meiring Naude sta. SM 171J, 33°20.0'S 28°12.7'E. Abbreviations as for Figure 1.

In *S. oualaniensis* (Fig. 1), for example, most of the club is taken up by the manus where the median suckers are much larger than the lateral ones, though the median suckers gradually reduce in size distally and proximally. On the dactylus, on the other hand, the sucker size reduces gradually from proximal to distal (except at the extreme tip where the suckers are subequal in size) and also from ventral to dorsal, i.e. the ventrolateral, ventromedial, dorsomedial, and dorsolateral suckers of one transverse row is each a little smaller than the last. As pointed out by Pfeffer (1912: 374) there is often a distinct difference in size between the median suckers of the manus and those of the dactylus, but in many cases this size difference is not so clear and it is difficult to determine the border between the two regions. It has, therefore, been found convenient to define the first dactyl row as that row in which the ventral lateral sucker is equal to, or larger in size than, the ventral median sucker.

In well-preserved specimens the suckers of the dactylus may easily be seen as being arranged in oblique transverse rows in which the dorsolateral, dorso-medial, ventromedial, and ventrolateral sucker is each situated a little more distally than the last, i.e. an imaginary line through the centres of the suckers forms an oblique, more or less straight line across the oral face of the club, with the dorsal end of the line being more proximal than the ventral end (Fig. 1). This arrangement continues almost to the distal tip of the club where the last one or two transverse rows may have only two or three suckers in each.

This interpretation of a transverse row may also be applied to the suckers of the manus and may be traced proximally even to the region where the suckers become more subequal in size. Ultimately, however, there remain a few proximal suckers that appear to have a general biserial rather than quadriserial arrangement and their number is remarkably constant, being five suckers on the right club and four on the left. These may be interpreted as constituting two pairs plus one odd (distal) sucker on the right club and one pair plus two odd (one proximal and one distal) suckers on the left, if the orientation of the biserial rows is to be the same as that of the quadriserial rows.

The distinction of the proximal group of biserial suckers from the quadriserial suckers is particularly clear in well-preserved specimens of moderate size (e.g. Fig. 3D); in very large specimens (and also in smaller specimens in a flaccid condition) the carpal region is frequently stretched, resulting in the irregular or scattered condition mentioned by Pfeffer (1912: 374). It has been found convenient to consider the biserial suckers as carpals and the quadriserial suckers, even when more or less subequal in size, as manus suckers. Though the median suckers of the first manus row are, indeed, not much bigger than the laterals, there is usually a discernible difference in size, which rapidly increases distally, and the quadriserial arrangement of the first manus row can always be traced by the position of the origin of the sucker stalks, even in cases where the suckers have been displaced.

Despite the very different descriptions of the carpal region by the authors

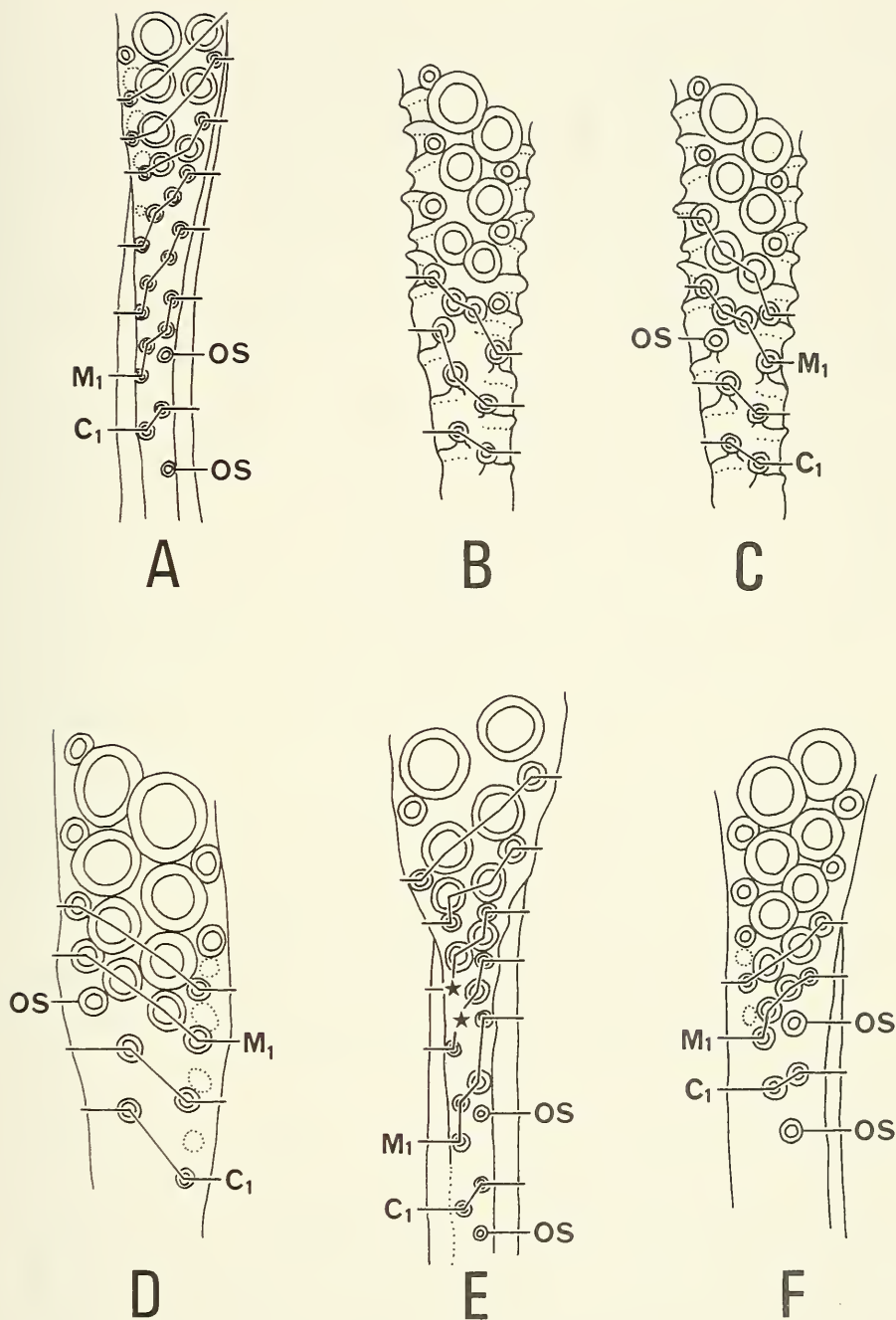


Fig. 3. Semidiagrammatic representation of the carpal region of various ommastrephid tentacular clubs, superimposed by the present interpretation of sucker arrangement. A. *Nototodarus gouldi*, left club of female, mantle length 218 mm (after Berry 1918). B. Sasaki's interpretation, and C. present interpretation of the right club of *Todarodes pacificus*, male, mantle length 255 mm (B and C after Sasaki 1929). D. *Sthenoteuthis pteropus*, right club of female, mantle length 365 mm (after Adam 1952). E. *Nototodarus sloani philippinensis*, left club of female, mantle length 180 mm (holotype) (after Voss 1963). F. *Ommastrephes bartramii*, left club of male, mantle length 303 mm (after Young 1972). Abbreviations as for Figure 1; stars indicate missing suckers.

cited above, an examination of their illustrations (Fig. 3) shows agreement with the basic ground-plan of sucker arrangement just described.

Berry's (1918, pl. 66 (fig. 2)) figure of *Nototodarus gouldi* illustrates the confusion that may arise when the proximal region of the club is stretched so that the subequal suckers of the first few manus rows appear to be more or less biserial. Nevertheless, their quadriserial origins may be traced (Fig. 3A), leaving four truly biserial carpal suckers since this is a left club.

Sasaki (1929) offered several alternative interpretations for the grouping of the proximal club suckers of *Todarodes pacificus* and illustrated the 2, 3, 4 interpretation (Fig. 3B). Of all his alternatives this is the closest to the present interpretation (Fig. 3C) of 2, 2, 1, 4 for the right club, though the row of four is here considered to pertain to the manus and not to the carpus.

Adam's (1952, fig. 47C) illustration of the carpal region of *Sthenoteuthis pteropus* shows the clear distinction between the biserial carpal and quadriserial manus suckers (Fig. 3D) and fully agrees with the ground-plan outlined above, whereas the club of *Nototodarus sloani philippinensis*, as illustrated in Voss (1963, fig. 28C), seems to differ markedly. However, this specimen (the holotype) has been re-examined and was found to have lost two suckers in the positions indicated in Figure 3E. Taking the missing suckers into consideration, it may be seen that the sucker arrangement of *N. sloani philippinensis* agrees with the above ground-plan, as does that of *Ommastrephes bartramii* (Fig. 3F) as illustrated in Young (1972, pl. 7M). Wormuth (1976) did not give illustrations of the tentacular clubs, but his description of the club of *S. oualaniensis* is applicable to Figure 1.

The presence of five right and four left biserial carpal suckers has been observed to predominate in all species of ommastrephids, with the exception only of *Hyaloteuthis pelagica* (Bosc), which seems to have fewer carpals on the right club. Very few specimens of *H. pelagica* have been examined thus far, but in the four right clubs seen the number of carpal suckers varied from one to three; the only left club examined had the usual four carpal suckers.

In the Ommastrephinae, the constant position of the fixing apparatus along the dorsal proximal margin of the club becomes even more clear if the fixing apparatus is considered as a unit consisting of alternating knobs and smooth ringed suckers. It has been found that the first (most proximal) element of the fixing apparatus may be either a knob or a smooth ringed sucker; most commonly, the fixing apparatus begins with a sucker on the right club and with a knob on the left club. It is, in fact, the position of the first smooth ringed sucker, rather than that of the first knob, that is constant.

The smooth ringed suckers of the fixing apparatus are actually modified carpal and/or lateral manus suckers and as such they also form part of the regular sucker arrangement of the club. Thus in *Sthenoteuthis oualaniensis* the first smooth ringed sucker of the fixing apparatus is also the first dorsal carpal sucker (Fig. 1). As the number of suckers (and knobs) in the fixing apparatus varies, this may also involve the modification of the more proximal dorsal

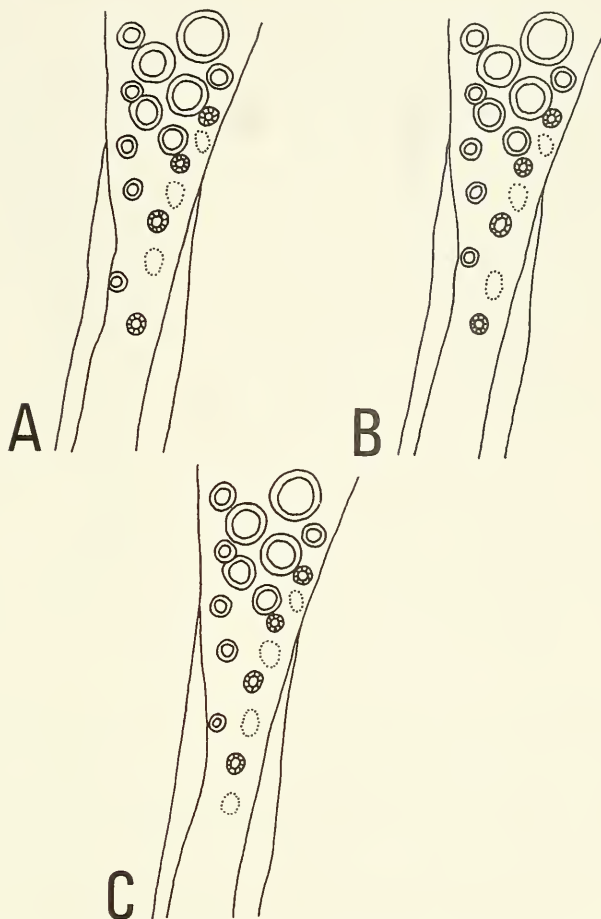


Fig. 4. Three possible variations of the fixing apparatus on the right club of *Sthenoteuthis oualaniensis*. A. First element of fixing apparatus, a sucker; two suckers proximal to the first knob. B. First element of fixing apparatus, a sucker; one sucker proximal to first knob. C. First element of fixing apparatus, a knob; no suckers proximal to first knob.

lateral suckers of the manus in specimens having a longer fixing apparatus, but the fixing apparatus always begins with the carpals in this species.

The position of the first knob of the fixing apparatus may be either proximal or distal to the first smooth ringed sucker (Fig. 4) and this has led to confusion in the past. If the first knob is distal to the first smooth ringed sucker (Fig. 4A–B), the number of suckers (regardless of type of dentition) proximal to this knob will be one (Fig. 4B) or two (Fig. 4A), depending on the position of the knob relative to the position of the ventral carpal suckers. If, however, the first knob is proximal to the first smooth ringed sucker (Fig. 4C), there are

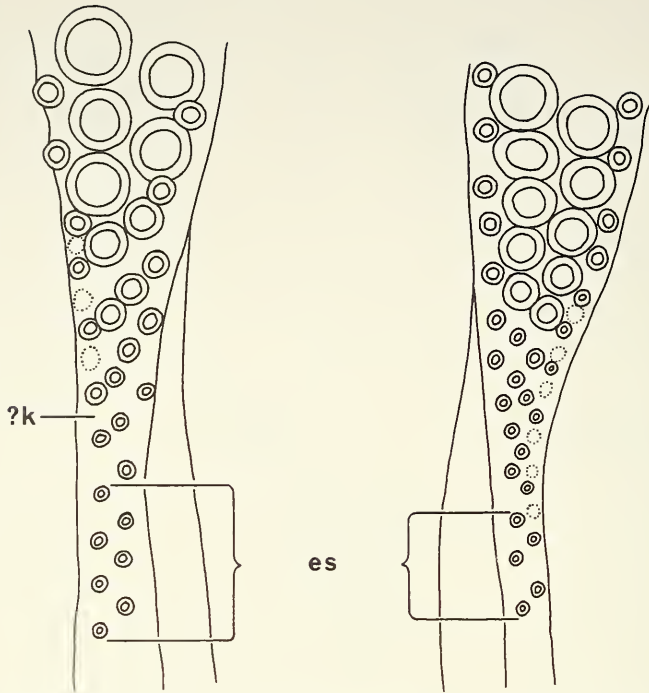


Fig. 5. Aberrant carpal condition in the tentacular clubs of *Sthenoteuthis pteropus* (after Adam 1952). es—extra suckers, ?k—knob presumably missing.

no suckers proximal to the knob. Thus past authors have stated that there are none to two suckers proximal to the first knob in *S. oualaniensis*. But if the position of the fixing apparatus is considered to be determined by the position of the first smooth ringed sucker, and if only the suckers in the dorsal longitudinal column are considered (the ventral carpals being ignored), then it may be seen (Figs 1 and 4) that in *S. oualaniensis* there are no suckers proximal to the first smooth ringed sucker in the dorsal column.

In the specimens examined, *Sthenoteuthis pteropus* and *Dosidicus gigas* (d'Orbigny) have the same type of club as *S. oualaniensis*, i.e. with the fixing apparatus beginning in the carpal region. There is, however, an aberrant condition (Fig. 5) that occasionally occurs. In these cases there appears to be a proliferation of the carpal suckers proximally and the regular arrangement is disrupted. Such a condition has been described and illustrated for *S. pteropus* by Adam (1952: 110, fig. 47F–G) and has been observed in several specimens of *S. oualaniensis* (Roeleveld unpublished). In Adam's specimen of *S. pteropus* there are five extra suckers on the right club; the left club has seven extra carpal suckers and also appears to lack at least one knob. The number of extra carpal suckers varies considerably in these aberrant specimens, which are otherwise indistinguishable from their conspecifics.

The club of *Ommastrephes bartramii* (Fig. 2) differs from that of *S. oualaniensis* (Fig. 1) in that the fixing apparatus is somewhat more distally placed. On the right club of *O. bartramii* the first smooth ringed sucker of the fixing apparatus is also the dorsal lateral sucker of the first manus row; on the left club the first smooth ringed sucker of the fixing apparatus pertains to the second manus row. Thus on both left and right clubs of *O. bartramii* there are two (toothed) suckers proximal to the fixing apparatus in the dorsal longitudinal column: the smooth ringed suckers of the fixing apparatus are all modified lateral manus suckers and the carpal suckers do not participate in the fixing apparatus. In *S. oualaniensis*, on the other hand, the fixing apparatus always begins with the carpus and the lateral manus suckers are involved only if the fixing apparatus includes more than one (left club) or two (right club) smooth ringed suckers. Put another way, if the dorsal longitudinal column of suckers alone is considered, there are two dorsal suckers proximal to the fixing apparatus in *O. bartramii* and none in *S. oualaniensis*.

The aberrant clubs occasionally found in *S. oualaniensis* and *S. pteropus* cannot be confused with those of *O. bartramii*, as in the aberrant condition the fixing apparatus usually begins in the carpal region, and the extra carpal suckers have smooth rings. In *O. bartramii* the carpal suckers are not involved in the fixing apparatus and have teeth on the distal part of the ring.

DISCUSSION

Since the primary function of the tentacular clubs is to capture active prey, any particular arrangement of the suckers presumably has a functional advantage. As the left and right clubs act together, the sucker arrangement of the two clubs may be seen in relation to each other if the mirror image of one is superimposed on the direct representation of the other (Fig. 6). When seen in this mutual relationship, the sucker arrangements present a number of interesting points. As first noted by Steenstrup (1857: 120) the knobs of the fixing apparatus of one club lie opposite the smooth ringed suckers of the other. Secondly, the carpal suckers not involved in the fixing apparatus, and hence with toothed rings, lie opposite the spaces between the suckers of the opposing club. Thirdly, the toothed suckers of the manus do not lie exactly opposite each other but are staggered, so that it is less likely that a sucker of one club will adhere to a sucker of the other club, as would happen if they were exactly opposite each other. The firm grip of two exactly opposed toothed suckers would presumably be difficult to release and would hamper the true function of the clubs, which is to grasp prey.

On the basis of this mutual relationship of the opposing club suckers, a reconstruction of the function of the ommastrephid clubs may be attempted. When the tentacles are extended to seize prey they would presumably be joined along the dorsal proximal edge of the clubs by the fixing apparatus, ensuring that both tentacles are extended to the same length and reach the prey at the

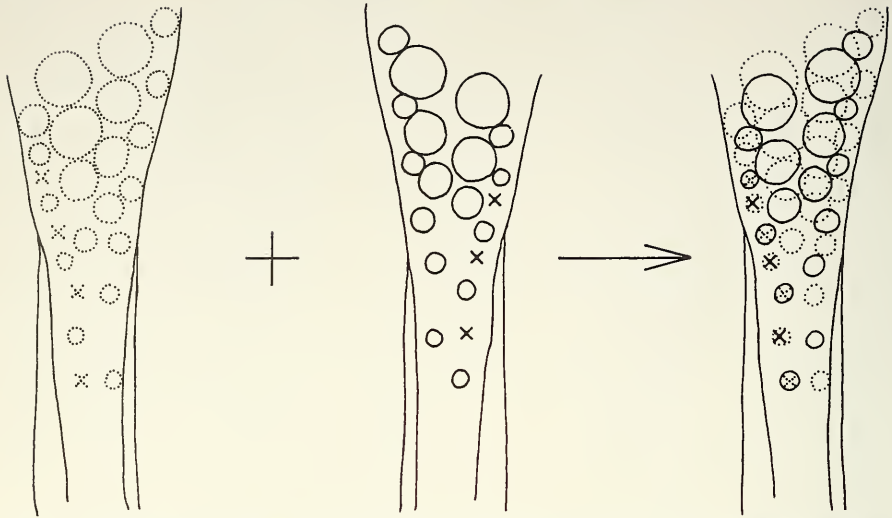


Fig. 6. Diagrammatic representation of sucker relationships in the proximal region when the left and right clubs of *Sthenoteuthis oualaniensis* are placed face to face. Circles represent suckers, crosses represent knobs: suckers and knobs of left club dotted, those of right club entire.

same time. The prey may then be captured by a tong-like action of the joined clubs, as has been recorded photographically (Baker 1957, fig. 3a).

Lane (1960: 38) has suggested that the united strength of the tentacles may then be used to drag in the prey. This more efficient use would then presumably enable the capture of larger or more active prey than if the tentacles were less co-ordinated. Kristensen (1981 pers. comm.) does not agree with Lane's suggestion and believes that if the clubs were still joined together on retraction it would hamper the regular contraction of the tentacular stalks.

Kristensen (1981 pers. comm.) has suggested that the fixing apparatus may also be used to hold the clubs within the cone formed by the circumoral appendages (arms plus tentacles) for streamlining while swimming.

The development of teeth on the horny rings of the suckers is considered to be an advanced condition and would be a distinct advantage in fast swimming squids feeding on active prey, since the teeth of the sucker rings ensure a firm grasp as they dig into the tissues of the prey. With the development of the fixing apparatus, however, a number of suckers are set aside to grasp not the prey but the knobs on the opposing tentacle of the squid itself. It would then be an advantage if the sucker rings were smooth and not toothed. Thus the smooth ringed suckers of the fixing apparatus have undergone a secondary loss of teeth, so that in the region where the clubs adhere to each other the possibility of self-inflicted damage is eliminated. Further adhesion of the clubs to each other is minimized by the staggered positions of the toothed suckers. Once the prey has been captured, the fixing apparatuses of the clubs may be rapidly separated by release of the vacuum in the sucker chambers.

ACKNOWLEDGEMENTS

This study is based upon material in the South African Museum and from numerous other institutions whose personnel provided access to material and facilities for study. I should like to thank G. L. Voss, Rosenstiel School of Marine and Atmospheric Science, University of Miami; J. H. Wormuth, Department of Oceanography, Texas A & M University; C. F. E. Roper and M. J. Sweeney, Division of Mollusks, National Museum of Natural History, Washington, D.C.; C. C. Lu, previously of the Department of Biology, Memorial University of Newfoundland and now at the National Museum of Victoria, Melbourne, Australia; M. R. Clarke, Laboratory of the Marine Biological Association of the U.K., Plymouth; P. M. David, Institute of Oceanographic Sciences, Wormley, U.K. and N. MacLeod, previously of that institution; J. Knudsen, Zoological Museum, Copenhagen and T. K. Kristensen, previously of that museum and now at the Danish Bilharziasis Laboratory, Charlottenlund; P. Bouchet and F. Danrigal, Laboratory of Malacology, National Museum of Natural History, Paris; J. M. Rosada and M. E. Cunha, Department of Pollution and the Environment, National Institute of Fisheries Investigation, Lisbon; W. Adam and J. van Goethem, Department of Recent Invertebrates, Royal Institute of Natural Sciences of Belgium, Brussels; and F. C. Naggs, Mollusca Section, British Museum (Natural History), London.

My sincere thanks go to M. A. Cluver and V. B. Whitehead of the South African Museum and G. M. Branch of the University of Cape Town for reading the manuscript and for their useful comments and criticisms. I should also like to thank C. F. E. Roper of the National Museum of Natural History, Washington, D.C., and T. K. Kristensen of the Danish Bilharziasis Laboratory, Charlottenlund, for their comments on the manuscript.

REFERENCES

- ADAM, W. 1952. Céphalopodes. *Result. scient. Expéd. océanogr. belge Eaux côt. afr. Atlant. Sud* 3: 1-142.
- BAKER, A. DE C. 1957. Underwater photographs in the study of oceanic squid. *Deep Sea Res.* 4 (2): 126-129.
- BERRY, S. S. 1918. Report on the Cephalopoda obtained by the F.I.S. 'Endeavour' in the Great Australian Bight and other southern Australian localities. *Zool. (biol.) Results Fish. Exp. 'Endeavour'* 4 (5): 201-298.
- LANE, F. W. 1960. *Kingdom of the octopus. The life history of the Cephalopoda*. New York: Sheridan House.
- LESSON, R. P. 1830. Mollusques. In: LESSON, R. P. & GARNOT, P. 1826-1830. *Zoologie du voyage autour du monde . . . sur . . . la Coquille pendant . . . 1822-25 . . . Par M. L. I. Duperry, etc.* 2: 239-246. Paris.
- PFEFFER, G. 1900. Synopsis der oegopsiden Cephalopoden. *Mitt. naturh. Mus. Hamb.* 17 (2): 145-198.
- PFEFFER, G. 1912. Die Cephalopoden der Plankton-Expedition. *Ergebn. Atlant. Ozean Planktonexped. Humboldt-Stift.* 2: 1-815.
- SASAKI, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *J. Coll. Agric. Hokkaido imp. Univ.* 20 (suppl.): 1-357.
- STEENSTRUP, J. 1855. Kjaeber af en kolossal Blaeksprutte. *Overs. K. danske Vidensk. Selsk. Forh.* 1855: 199-200. In: VOLSØE, A., KNUDSEN, J. & REES, W., trans. 1962. *The cephalopod papers of Japetus Steenstrup*: 14-15. Copenhagen: Danish Science Press.

- STEENSTRUP, J. 1857. Hr. Professor Steenstrup foreviste og karakteriserede derpaa et Par nye Cephalopoder. *Vidensk. Meddr dansk naturh. Foren.* **1856**: 120. In: VOLSØE, A., KNUDSEN, J. & REES, W. trans. 1962. *The cephalopod papers of Japetus Steenstrup*: 16. Copenhagen: Danish Science Press.
- VERRILL, A. E. 1878. Notice of recent additions to the marine fauna of the eastern coast of North America. *Am. J. Sci.* (3) **16**: 207-215.
- VERRILL, A. E. 1880. The cephalopods of the North-eastern Coast of America. Part I. The gigantic squids (*Architeuthis*) and their allies; with observations on similar large species from foreign localities. *Trans. Conn. Acad. Arts Sci.* **5**: 177-257.
- VOSS, G. L. 1963. Cephalopods of the Philippine Islands. *Bull. U.S. natn. Mus.* **234**: 1-180.
- WORMUTH, J. H. 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. *Bull. Scripps Instn Oceanogr.* **23**: 1-90.
- YOUNG, R. E. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. *Smithson. Contr. Zool.* **97**: 1-159.
- YOUNG, R. E. & ROPER, C. F. E. 1968. The Batoteuthidae, a new family of squid (Cephalopoda: Oegopsida) from Antarctic waters. *Antarct. Res. Ser.* **11**: 185-202.
- ZUEV, G. V., NESIS, K. N. & NIGMATULLIN, CH. M. 1975. System and evolution of the squid genera *Ommastrephes* and *Symplectoteuthis* (Cephalopoda, Ommastrephidae). *Zool. Zh.* **54**: 1468-1479 (in Russian, with English abstract).